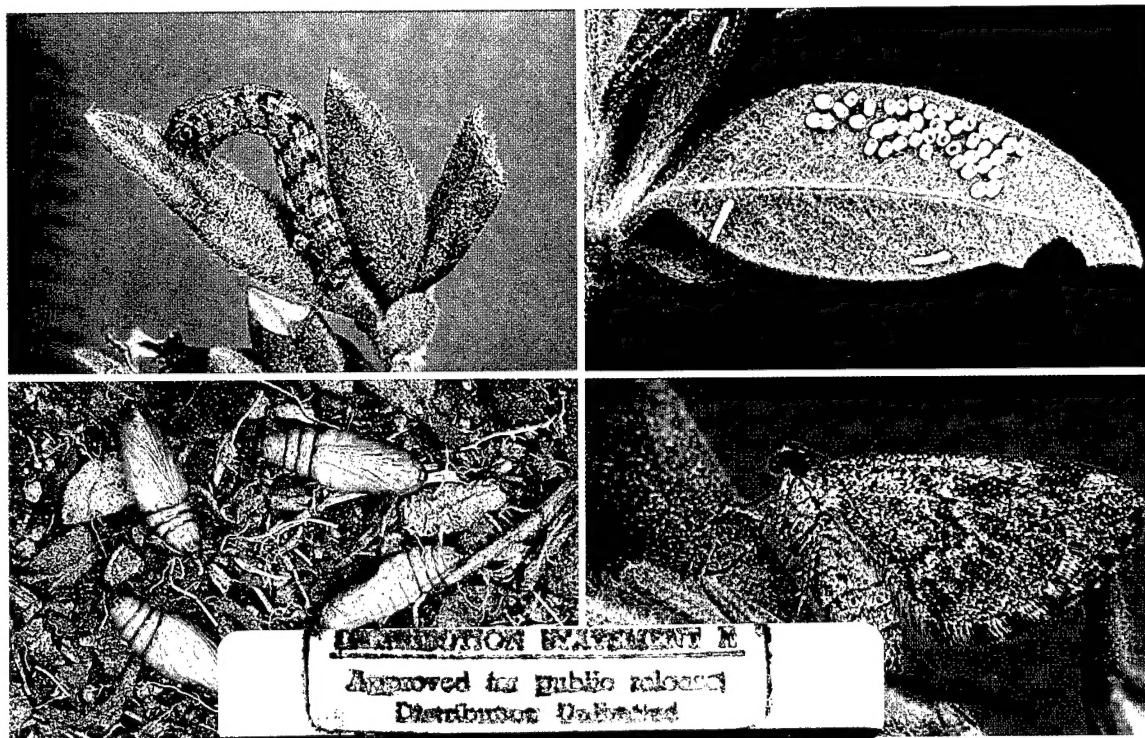




Taxonomy, Life History, and Ecology of a Mountain-mahogany Defoliator, *Stamnodes animata* (Pearsall), in Nevada



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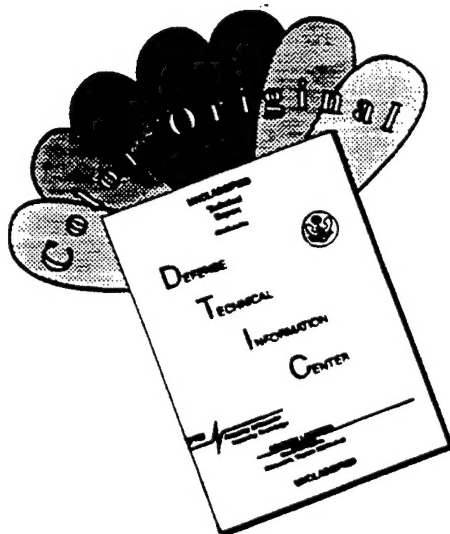
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Mountain-mahogany Defoliator,
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By Malcolm M. Furniss
Douglas C. Ferguson
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J. Wayne Burkhardt
Arthur R. Tiedemann
John L. Oldemeyer

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Foreword

Shrub entomology is a neglected field but insects are important to resource management and to shrub improvement research. This study is the most comprehensive one known to us concerning an insect on a native western shrub. The attention given to ecological factors and interactions between the insect, shrub, and other community components is uncommon if not unique. So, too, is the inclusion of original taxonomic work in a broad-based paper dealing with biological and ecological aspects of an insect. We hope that our effort will stimulate similar if not nobler work on other shrub insects.

This publication is dedicated to Robert L. Furniss (1908–80), who knew well the forests and shrubs of the West, and their insects.

Taxonomy, Life History, and Ecology of a Mountain-mahogany
Defoliator, *Stamnodes animata* (Pearsall),
in Nevada¹

by

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Abstract

During 1978–79, larvae of a geometrid moth, *Stamnodes animata* (Pearsall), defoliated curlleaf mountain-mahogany (*Cercocarpus ledifolius* Nutt.) on 4,500 ha at Sheldon Wildlife Refuge, Washoe and Humboldt Counties, Nevada. Extensive tree mortality resulted. The genus *Stamnodes* Guenée is partly revised herein, and *animata* is transferred to it from *Marmopteryx* Packard. Life stages and their habits are described. Moths were present from late May to mid-July, with oviposition commencing in early June. Larvae were present from June until October and began descending to pupate in soil in late September. Population sampling is discussed. Eggs were parasitized by three species of wasps (*Telonomus* sp., *Trichogramma pretiosum* Riley, *T. exiguum* Pinto and Platner). Larvae were parasitized by an ichneumon wasp (probably *Netelia* sp.) and by two tachinid flies, *Patelloa plumiseriata* (A & W) and *Blondelia connecta* (Curran). Predacious tree-climbing ants (*Formica integroides planipilis* Creighton) played a major role in the much greater survival of mountain-mahogany at higher elevations than at lower areas, where ground-dwelling harvester ants (*Pogonomyrmex owyheei* Cole) were dominant. Densities of 10 key site-indicator species of passerine birds on defoliated transects are compared before defoliation and for 6 years afterward. Where tree killing was greater, bird densities fluctuated more, and two species—the gray flycatcher (*Empidonax wrightii*) and American robin (*Turdus migratorius*)—disappeared. Litter weight was 1,186 g/m² greater under defoliated than nondefoliated trees because of premature loss of looper-notched leaves. Susceptible stands are extensive in area; grow on litter-rich permeable soil; and lack *Formica* ants.

Curlleaf mountain-mahogany (*Cercocarpus ledifolius* Nutt.) is an evergreen, rosaceous, treelike shrub that grows in 10 western States (Fig. 1). Maximum recorded height is 7.3 m (24 feet). Multiple stems are typical; the bark on young trees is smooth and grayish white, and that of older trees is rough and dark gray. The tree is xerophytic; its leathery leaves have a shiny, thick cuticle, revolute lateral margins, and a pubescent underside. The flowers, which lack petals, bloom in May and June. The fruit is an achene that matures in late summer. When a fruit-laden tree is seen backlit by the sun, the feathery styles create an extraordinary visual effect (Fig. 2).

In high desert areas, mountain-mahogany provides welcome visual relief from an otherwise vast, monotonous landscape dominated by sagebrush. Ungulates such as cattle, domestic sheep, mule deer (*Odocoileus hemionus*), and mountain sheep (*Ovis canadensis*) utilize mountain-mahogany for browse, and it is especially critical to mountain goat (*Oreamnos americanus*) survival in Idaho (Kuck 1980). Deer seek out its protection during fawning and during the heat of the summer (Fig. 3). The unique habitat provided by mountain-mahogany also results in more birds frequenting it than other high desert ecological sites.

In late summer 1978, thousands of mountain-mahogany trees on 4,500 ha (1,821 acres) at Sheldon National Wildlife Refuge (NWR), Washoe and Humboldt Counties, Nevada, were defoliated by larvae of a geometrid moth. A damaging population of loopers recurred in 1979, after which the infestation subsided.

The insect was determined to be *Stamnodes animata* (Pearsall) and, because it had not been studied, we

sought information, which is reported herein. The taxonomic revision presented here, along with color photos and descriptions of the insect's life stages, will facilitate accurate identification when others encounter this insect in the future. Other information presented will aid resource managers in classifying the susceptibility of stands before infestation and in anticipating effects that a future infestation might have on the associated plant and animal communities.

Study Area

Sheldon National Wildlife Refuge is in Washoe and Humboldt Counties in northwestern Nevada. The Refuge's dominant management theme is to maintain the existing diversity of native wildlife species and other natural values of this high desert ecosystem. About 82% of the vegetative cover is sagebrush (*Artemisia* spp.). Mountain-mahogany occurs above 1,800 m, which is the average elevation of the Refuge, generally on relatively thin to moderately developed fertile soil. It is often associated with basalt outcrops, and commonly forms islands among stands of big sagebrush (*Artemisia tridentata* Nutt.) and various other vegetation.

Although mountain-mahogany occupies only 1% of the Refuge, it is important to many species of wildlife. In the midst of expanses of sagebrush, islands of mahogany provide for greater wildlife diversity and abundance than is otherwise possible. An important element of mahogany trees is their height, which enables them to provide shade for deer, and perches and nesting sites for birds. More than 75% of species of pas-

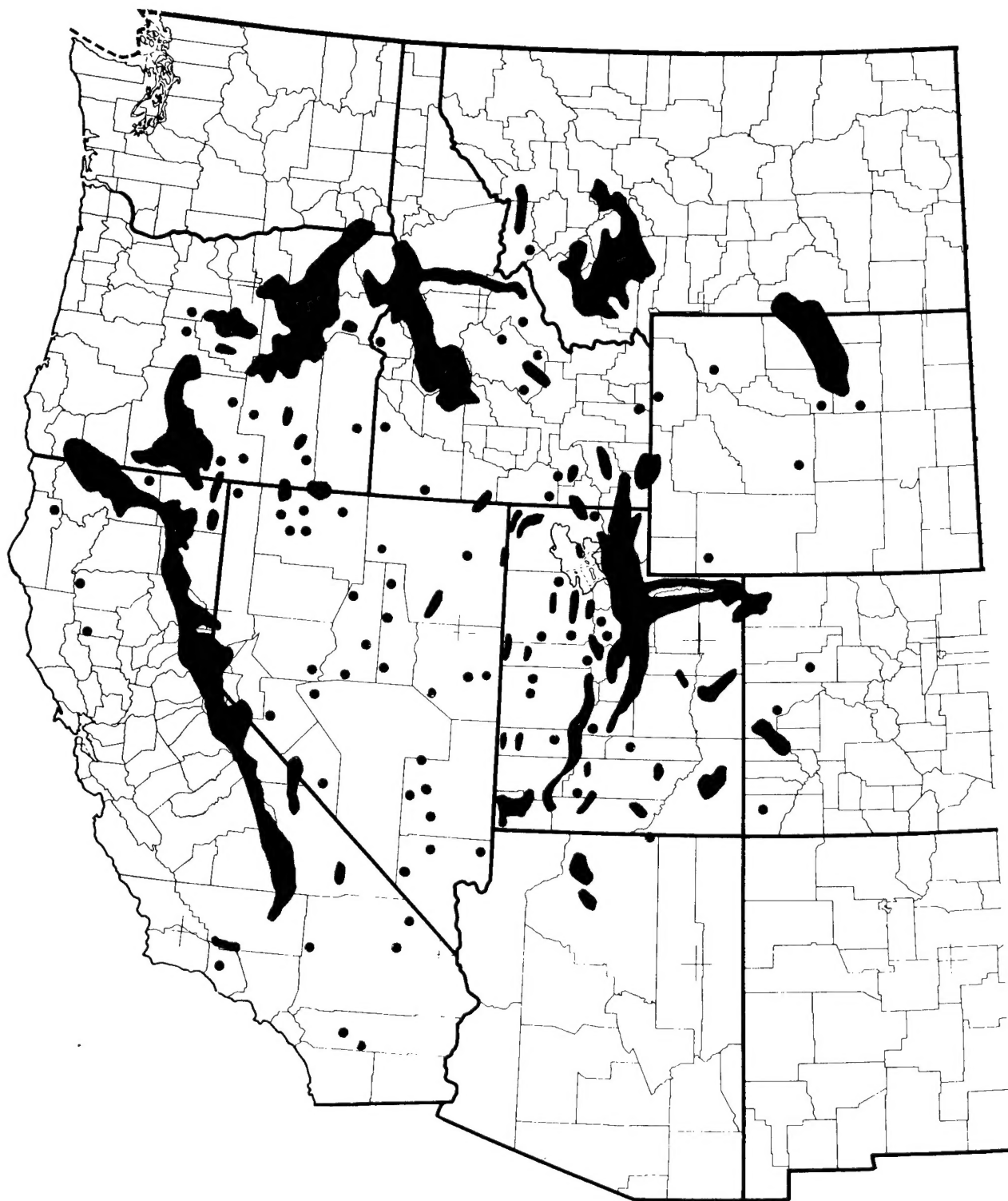


Fig. 1. Geographic distribution of curleaf mountain-mahogany, *Cercocarpus ledifolius* (from E. L. Little, Jr., U.S. Department of Agriculture, Forest Service, Misc. Publ. 1314 [1976]).



Fig. 2. Mountain-mahogany is an evergreen shrub with narrow leaves adapted to a semiarid environment; its abundant fruits have long, feathery styles.



Fig. 3. Mountain-mahogany is utilized for shelter and food by numerous wildlife including mule deer (*Odocoileus hemionus*), here seeking relief from summer heat.

serine birds occurring on the Refuge use mahogany stands in some fashion—more than any other ecological site.

Our studies were performed primarily at Badger Mountain (elevation 1,933 to 2,165 m). Additional observations and data, particularly relating to tree mortality, were obtained at Fish Creek Mountain (elevation 1,927 to 2,162 m). Trees at Badger Mountain were mostly older as shown by the tabulation derived from plots measured in 1979:

	Fish Creek Mountain	Badger Mountain
	(%)	(%)
Seedlings	31	11
Saplings	43	5
Mature trees	26	84

Average annual precipitation in the Badger Mountain study area varies from 28 to 38 cm. Average winter temperatures vary from -3 to -6°C , and average summer temperatures from 27 to 30°C .

Methods

Stamnodes animata-related

To determine the lasting effects of the 1978 defoliation, stands and individual trees were observed annually through 1981. Camera stations were located at Badger Mountain, from which comparative photos were taken in subsequent years. Included for observation were trees varying from undamaged to completely defoliated (Fig. 4).

Life stages of the insect were obtained by field collections and in the greenhouse, where adults were confined in cages containing potted mountain-mahogany plants.



Fig. 4. Trees varied in the degree of their defoliation and recovery. A few escaped defoliation (a); others recovered, but many died (b).



Fig. 5. Moth larvae were sampled by clipping branches (a) and by beating to dislodge larvae onto a sheet (b).

Loopers that hatched from eggs laid on the mountain-mahogany leaves were then reared to maturity. Molting of loopers was observed and samples of each instar were preserved for measurement of head capsule widths in order to classify field larvae by instar.

Seasonal history of *S. animata* was determined by weekly field collections in 1979 and 1981 between time of oviposition in June and completion of pupation in October. These collections also provided specimens for study of parasites of immature stages.

Moth abundance was determined by operating an ultraviolet light at night. Egg density was determined by collecting 30 leaves weekly from each of 10 different trees. Loopers were sampled weekly by two means: (1) clipping about 76 cm of each of three terminal branches (Fig. 5a) on each of 10 shrubs, then counting loopers on them, and (2) holding a 1-m² cloth beneath branches that were then struck sharply three times with a stick to dislodge insects (Fig. 5b). Insects obtained from three branches per tree were pooled and the average number of loopers per 10 shrubs was determined. In-

stars of collected larvae were determined by measuring the widths of their head capsules with a microscope equipped with an ocular disc inscribed with a graduated 1-cm line.

Ants

The relation of ants to *Stamnodes* infestation was determined initially by comparative field observation of defoliated and nondefoliated trees and stands. Thereafter, predation by *Formica* ants (Fig. 6) was measured by comparing survival of loopers placed on two pairs of branches; one member of each pair had a sticky ant-barrier and the other was left untreated.

The relation between tree mortality and ants was determined in 1982 on four transects of varying elevation and location. Trees were rated by four degrees of damage (undamaged, <50% dead, >50% dead, and all dead). Sample trees were selected by walking 20 steps into a stand, then selecting the nearest tree in each quarter of the surrounding circle. The next sample point was selected by locating the nearest mountain-mahogany in the

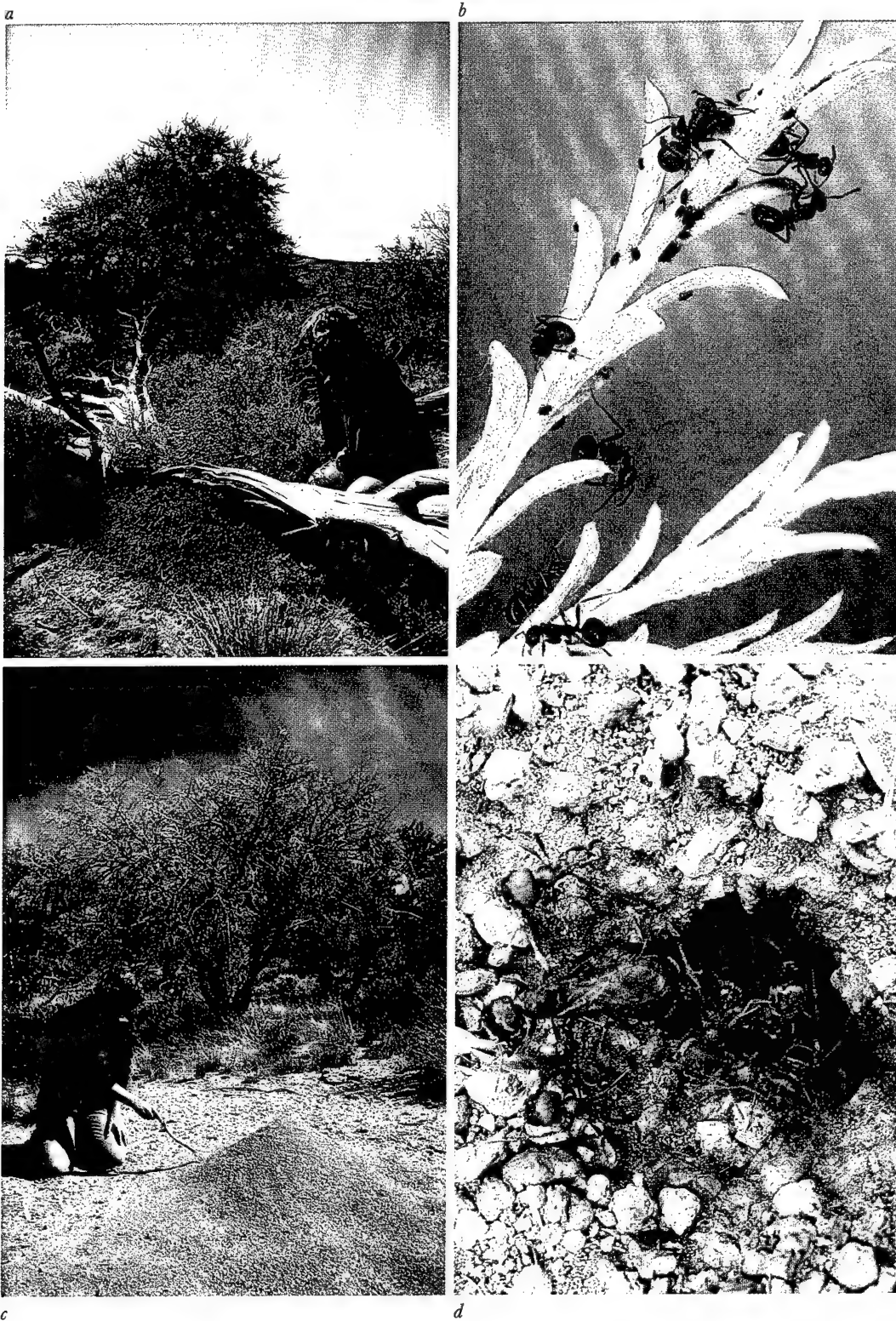


Fig. 6. Species of ants differed in the defoliated area. Higher up, tree-climbing *Formica* ants (a,b) preyed on moth larvae, saving a majority of trees. Lower down, ground-dwelling *Pogonomyrmex* harvester ants (c,d) were dominant and a majority of trees died from repeated defoliation.

forward 180° arc and walking 20 steps in that direction to the next sample point. Ant nests visible from each sample tree were tallied and identified as being those of *Pogonomyrmex* or *Formica* (Fig. 6).

Passerine Birds

By good fortune, four paired, 100-m × 1-km (10-ha) transects were established in 1978, two each at Badger Mountain and Fish Creek Mountain, before the loopers had defoliated mountain-mahogany trees. Of the two areas, Fish Creek Mountain was rated of better range condition, being more mesic and having a richer, more diverse understory. Beginning in 1978, we censused passerine birds in June and July during the peak breeding season, by walking the center line of each transect at daylight for 3 consecutive days during each of three intervals within a 30-day period. The direction of walking was reversed each subsequent day. Birds were identified by sight and sound, and nests were recorded by species. Densities of bird species were expressed as the average number counted per locality (20 ha) per day.

Soil Enrichment and Litter Deposition

We were unaware of the outbreak in time to measure the soil enrichment that resulted from a sudden conversion of accumulated foliage to excrement in 1978. However, in 1980, soil and litter samples were taken beneath 17 trees that had been defoliated and from beneath 17 mahogany trees that had not been defoliated. Litter was oven dried and expressed as grams per square meter. Total nitrogen (N), phosphorus (P), and sulfur (S) in litter and soil were determined by analytical techniques described in Tiedemann and Furniss (1985). We also measured the availability of N, P, and S in soil from the surface to 3–4 cm beneath defoliated and nondefoliated trees using a pot culture technique (Jenny et al. 1950).

Plant Community Response

Short-term growth response of understory plants, mainly Idaho fescue, was observed and photographed. Long-term changes in the proportional canopy cover of shrubs, grasses, and forbs will be determined from 12 vegetation transects established in 1979 and 1980 at Badger Mountain and Fish Creek Mountain. Each transect consisted of a 3.0-m × 30.5-m macro-plot. Canopy cover was measured on a line intercept transect along a 30.5-m side of the plot. Mahogany trees were counted within the 93-m² macro-plot. Other shrub

species were counted on a 0.9-m × 30.5-m plot oriented lengthwise along the macro-plot. Herbaceous plants and shrub seedlings were counted on 10, 0.3-m × 0.46-m subplots uniformly spaced along each 30.5-m line intercept transect.

Taxonomy of *Stamnodes animata* (Pearsall)¹

Tribe *Stamnodini*

Stamnodes Guenée is one of several genera of the subfamily Larentiinae included in the tribe *Stamnodini*, a group that occurs mainly in the Western Hemisphere, and which is represented north of the Mexican border by about 40 species. Thirty-five of these are now considered to belong to the genus *Stamnodes*, four to *Stamnoctenis* Warren, and one to the essentially neotropical genus *Heterusia* Hubner. Because these moths have never been reviewed or revised taxonomically, it seemed advisable to make at least a preliminary review of the group for background information and to ensure that *animata* will be assigned to the correct genus.

Although the group is poorly known both taxonomically and biologically, host information is available for several other species. The following have been reared from birchleaf mountain-mahogany, *Cercocarpus betuloides* Nutt. (Rosaceae): *Stamnodes annellata* (Hulst), *S. coenonymphata* (Hulst), and *S. ululata* Pearsall in Los Angeles County, California (data from reared adults in C. Henne collection, Natural History Museum of Los Angeles County), and *S. marinata* Wright in southwestern Oregon (McFarland 1975). Other recorded hosts for species of *Stamnodes* are *Purshia glandulosa* Curran (Rosaceae) for *S. tessellata* (Packard); *Salvia mellifera* Greene and *Salvia apiana* Jepson (Lamiaceae) for *S. affiliata* Pearsall; *Phacelia cicutaria* Greene (Hydrophyllaceae) for *S. albiapicata* Grossbeck; *Pholistoma auritum* Lindl. (Hydrophyllaceae) for an unidentified *Stamnodes* sp. near *albiapicata* (all from southern California, C. Henne collection); waterleaf, *Hydrophyllus tenuipes* Heller (Hydrophyllaceae) for *S. blackmorei* Swett on Vancouver Island (Hardy 1961); and boneset? [possibly *Eupatorium perfoliatum* L. (Asteraceae)] for *S. gibbicostata* (Walker) [under the synonymic name *Strigularia* (Minot)] in New York State (Bruce 1887).

Eggs of a species identified as *Stamnodes cassinoi* Swett were illustrated by Peterson (1968), without source or host given. *Stamnoctenis morrisata* (Hulst), the type-species

¹By Douglas C. Ferguson.

of a closely related genus, has been reared several times. The larva was described by McGuffin (1958), who reported the host as Rocky Mountain juniper, *Juniperus scopulorum* Sarg. Rocky Mountain juniper was again reported as the host in British Columbia by Prentice et al. (1963). The present author reared *S. morrisata* at the Great Basin Experiment Station, Ephraim, Utah, in 1980, also on a species of juniper, which genus may prove to include the hosts of all species of *Stamnoctenis*. Thus, of the 40 recognized species of *Stamnodini* in this country or Canada, hosts have been reported for 11, and the immature stages described for only 3.

Although the *Stamnodini* are close to and perhaps not really distinct from the large, worldwide tribe *Hydriomenini*, they mostly form a coherent, easily recognized group containing many closely similar species with common features of structure, color, and wing pattern. A few *Stamnodini* are brightly colored on the uppersides of the wings, usually in shades of orange, bright yellowish brown, or reddish brown—e.g., *S. topazata* (Strecker), *S. artemis* Rindge, *S. splendorata* Pearsall, and *S. fervefactaria* (Grote)—but the majority have plain, light-brown wings, also unmarked on the upperside or with only a diffuse postmedial band of a shade somewhat lighter or darker than the ground color.

A distinctive feature of members of the tribe is their tendency to display a more elaborate, specialized wing pattern on the underside than on the upperside. This is a cryptic pattern that may appear frosted, mottled, or reticulated in a manner resembling natural backgrounds. Unlike most geometrid moths, which rest with their wings held horizontally, the *Stamnodini* hold their wings together above their backs, in butterfly fashion (cover photo), exposing the cryptically marked undersides. Indeed, their appearance and mannerisms bring to mind certain satyrine butterflies of the genera *Oeneis* and *Coenonympha*, which led to the naming of a common California species *Stamnodes coenonymphata*. Unlike butterflies, most species are nocturnal, although at least one of the brightly colored ones of the Northwest, *S. topazata*, seems to be entirely diurnal, flying in bright sunshine.

Genus *Stamnodes* Guenée

Stamnodes Guenée, 1857, in Boisduval and Guenée, Histoire naturelle des Insectes, Species général des Lépidoptères 10:515.

Type-species: *Fidonia pauperaria* Eversmann, 1848, by monotype. Central Asia.

Marmopteryx Packard, 1874, in F.V. Hayden, Annu. Rep. U.S. Geol. Geogr. Surv. Terr.

1873:552. NEW SYNONYMY.

Type-species: *Marmopteryx tessellata* Packard, 1874, ibidem: 552, Fig. 6, designated by Kirby, 1878. Southwestern U.S.A.

The *Stamnodini* of temperate North America were, until now, divided among three genera, *Stamnodes*, *Marmopteryx*, and *Stamnoctenis*, according to the following simple criteria: those with a foretibial spine were referred to *Marmopteryx*, those without the spine but with bipectinate male antennae to *Stamnoctenis*, and everything else to *Stamnodes*. *Stamnodes animata*, having a sharp terminal spine on the foretibia (Fig. 7a), has always been included in *Marmopteryx*. But even the most cursory examination of other character systems, especially the genitalia (not comprehensively studied by earlier authors, although providing exceptionally good characters), shows that this scheme does not work, because other features do not vary in concordance.

Certain structural modifications commonly used as key characters for adult geometrid, noctuid, and other moths, such as those of the antenna and foretibia cited above, are clearly plastic and readily evolved habitat-related features that have come and gone, or that have been modified repeatedly and independently countless times. They may not in themselves have any profound significance in terms of phylogenetic relationship at generic or higher levels, although they are extremely useful for distinguishing species. The function of the foretibial spine or claw is not definitely known, but inasmuch as it occurs most frequently in desert species, it is thought to aid the moths in emergence in dry, consolidated soils. In some noctuid moths of arid habitats it is developed as a more obviously fossorial claw (e.g., in species of *Schinia*); that of *animata* appears rudimentary by comparison.

Three of the four species that were included in *Marmopteryx*, namely *tessellata*, *animata*, and *marmorata* Packard, are not as closely related to one another as each is to some other species of *Stamnodes* (the fourth, *watsoni* Cassino, may be the same species as *marmorata*). Their common possession of a foretibial spine may be a result of convergence. As both male and female genitalia and general facies of adult moths suggest taxonomic relationships quite at variance with the presence or absence of the foretibial spine, there is no choice but to relegate *Marmopteryx* to the synonymy of *Stamnodes*, an action that was not taken in the new *Check List of the Lepidoptera of America North of Mexico* (Ferguson in Hodges et al. 1983) because the revisionary research had not been done when that work was written.

Stamnoctenis is retained for *morrisata* (Hulst), *rubrosuffusa* (Grossbeck), *pearsalli* (Swett), and *vernon* Guedet,

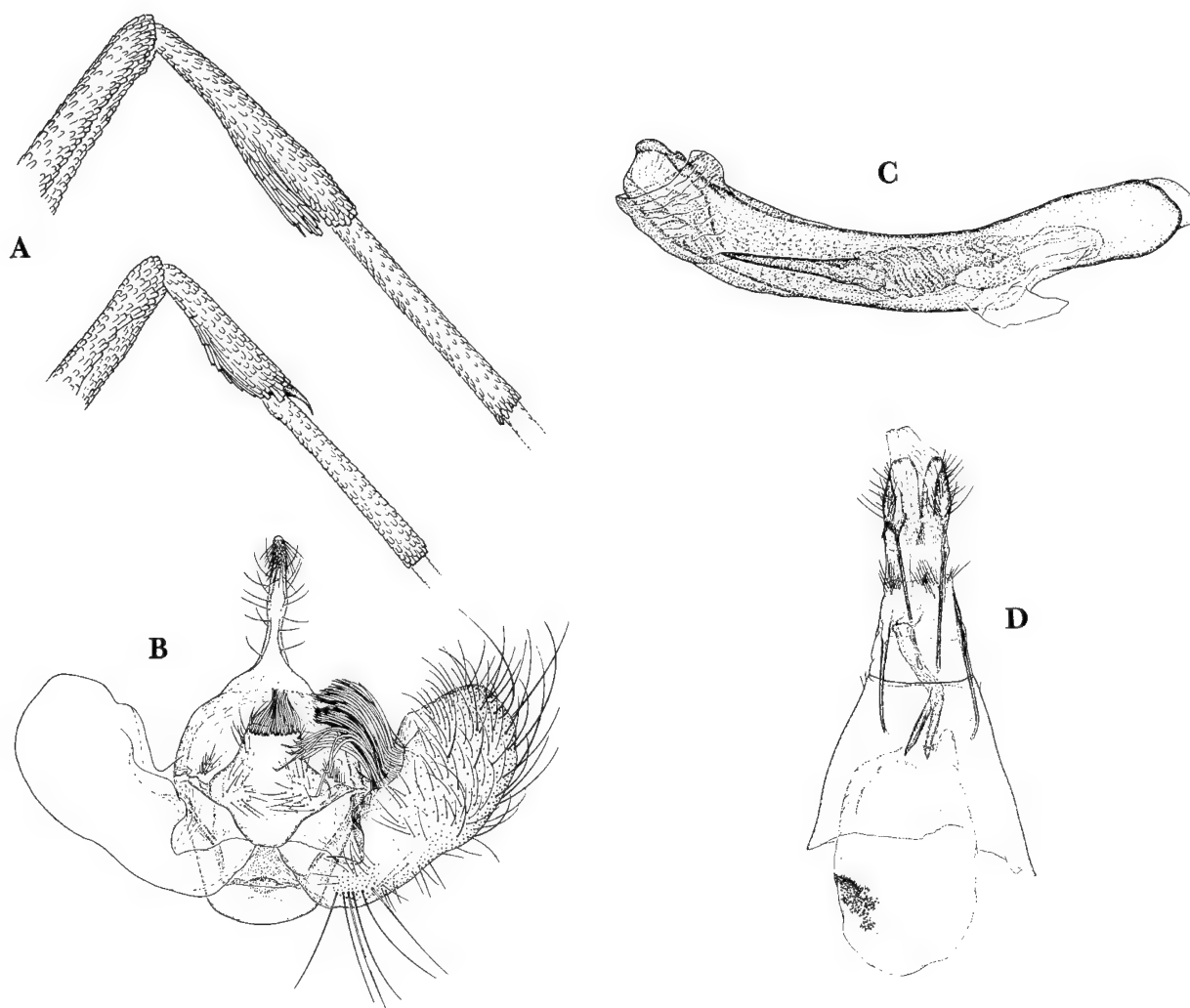


Fig. 7. Distinctive features of *Stamnodes animata* include a foretibial spur (a) and the characteristics of the male (b,c) and female (d) genitalia.

because of differences in genitalia, elongated wing shape, and characteristic wing pattern. The remaining names appearing under *Stamnoctenis* in the Check List—*ululata* Pearsall, *similis* W.S. Wright, *costimacula* (Grossbeck), *kelseyi* W. S. Wright, and *pallula* (McDunnough), all probably representing only two species—are hereby transferred provisionally to *Stamnodes*. The parentheses for authors' names reflect these new or revised combinations with *Stamnodes*.

Aside from the 33 recognized species of *Stamnodes* that occur in the western United States, the genus is represented by only 1 species in eastern North America, 10–12 seemingly related species in Mexico and the neotropics, and 3 in central Asia between the Caucasus and northern China (one of which reaches Japan).

The type-species of *Stamnodes*, *S. pauperaria* (Eversmann), is a central Asian species described from the

USSR. Two specimens, a male and female from the Altai Mountains, Mongolia, were found in the collection at the U.S. National Museum of Natural History, and an immediate comparison with North American species could be made. *Stamnodes pauperaria* seems to agree in every respect with the American species referred to as *Stamnodes*, except that the eighth sternite of the male has a pair of sharp, thornlike processes on its posterior margin, unlike any nearctic species examined.

Perhaps more by chance than relationship, the male genitalia of *pauperaria* are remarkably similar to those of *fervefactaria* (Grote); the female genitalia are almost indistinguishable from those of several American species. The moth is yellow, almost as bright as *S. splendrata* Pearsall from Arizona, but with a pattern that suggests *S. coenonymphata* (Hulst). It lacks the foretibial spine. The similarities are such that *pauperaria* and our

species, including *animata*, may with confidence be treated as congeneric.

Stamnodes animata (Pearsall),
New Combination

Marmopteryx animata Pearsall, 1906, Brooklyn Inst. Sci. Bull. 1(8):212.

Type-locality: Beaver Canyon, Utah [holotype in U.S. National Museum].

Description

Adults (*cover*; Fig. 10) of *S. animata* may be described briefly as follows: upperside of wings plain, light grayish brown, almost without markings; underside of hindwing and part of forewing toward apex variably frosted with white or nearly white scales, heavily to almost solidly so in females, much less so in males, and underside of hindwing with strongly convex, thin, dark-brown transverse band at or before middle of wing, angled near middle, curving distad toward inner margin; antennae of both sexes simple, that of male compressed, setose, but not pectinate; frons strongly protuberant, covered with a dense mat of short, light- or dark-colored scales that incline inwardly from each side toward the unscaled midline; labial palpus very short, hardly extending beyond base of tongue; foretibia of both sexes with sharp terminal spine on anterior side (Fig. 7a), variable in length but always present (somewhat reduced in southern specimens).

Note especially that the color and pattern of the underside of the hindwing plus the presence of a foretibial spine represent a unique combination that serve to distinguish *animata* from all other Geometridae in North America. Two or three other species of *Stamnodes* may resemble *animata* closely, especially *S. modocata* W. S. Wright, but these always lack the foretibial spine (Fig. 7a) and have different genitalia. The length of the forewing in Oregon, Utah, and most of Nevada is 13–16 mm for males and 11–16 mm for females. It is larger in Clark County, Nevada, and southern California, where wing length may reach 19 mm in the largest individuals.

Male genitalia (Fig. 7b) are with simple uncus (not strongly dilated or spatulate), a large bristle tuft on each valve, a pentagonal juxta with posterior side bearing transverse row of stout bristles, and a single large spine in aedeagus (Fig. 7c). Female genitalia (Fig. 7d) are not as distinctive as those of male, but demonstrate a characteristically irregular signum bearing numerous papillae on inner side.

Distribution

One hundred forty-three adults of *S. animata* were examined from localities in Utah, Nevada, eastern Oregon, and eastern and southern California with labels inscribed with elevations of 6,100 feet to 8,000 feet (1,860 m to 2,440 m). Additional information was provided by F. H. Rindge (personal data) for another 115 specimens from the same general region in the collection of the American Museum of Natural History, New York. The northernmost locality is Baker, in Baker County, Oregon, and the southernmost is Wrightwood (6,100 feet), in San Bernardino County, California. Collection records for adults are known from the following States and counties: Nevada—Washoe, Humboldt, Elko, Lander, Clark; Utah—Tooele, Utah, Garfield, Piute; Oregon—Baker, Harney, Klamath; and California—Modoc, Siskiyou, Mono, Tulare, Inyo, Kern, Los Angeles, San Bernardino. Apart from the study area in Nevada, only one larval collection record is known: 10 miles west of Panguitch, in Garfield County, Utah, where adults emerged 19 June 1969 from larvae collected September 1968 on *Cercocarpus ledifolius* (M. M. Furniss, personal data).

Flight period

Adults fly mainly in June, but there are records for as early as 12 May (Clark County, Nevada), 20 May (Wrightwood, California), and 31 May (Bly Mountain, Oregon), and as late as 15 July (Fish Lake, Steens Mountains, Oregon), and 17 July (Kingston Camp, Lander County, Nevada). Adults were collected from 29 June to 13 July at Red Canyon Camp, Garfield County, Utah (F. H. Rindge, in correspondence). The wide variation in emergence times indicated by these dates probably reflects local climatic differences and elevation. It should be noted that the superficially similar *S. modocata* flies much later, from 26 August to 8 October.

Description of Immature Stages

Egg

The egg (*cover*; Fig. 8a) is 0.85 mm long (SD = 0.04 mm; $n = 30$) \times 0.55 mm wide (SD = 0.03 mm; $n = 30$), flattened slantwise at the micropyle-bearing end, and rounded at the other end, where it attaches to the leaf. The chorion has a luster and is finely granular at low magnification. At high magnification, the chorion looks porous, being densely punctured with pits surrounded by thick, raised walls (Fig. 8b) and the micropyle appears as though it were branded in wax.

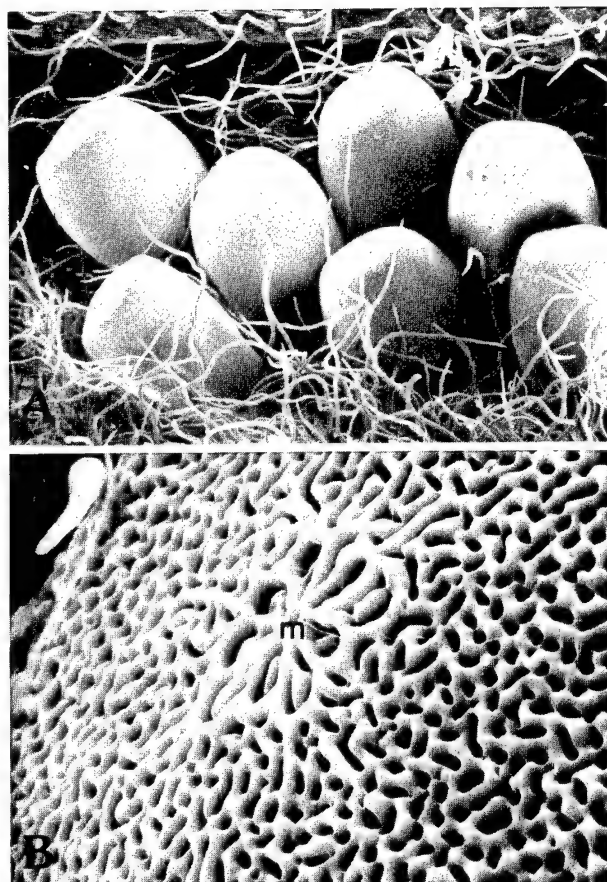


Fig. 8. Eggs of *Stamnodes animata* ($\times 50$) were laid on the pubescent underside of leaves (a). The chorion and micropyle (m) appeared waxlike and porous at $\times 600$ magnification (b).

Eggs are light yellow initially but turn darker yellow with age. Just before hatching, the shell is whitish and the yellowish larva is visible within, curled into a U-shape with its ends facing the micropyle. Upon eclosion, the larva cuts off the end of the egg shell cleanly and flush with the side.

Larva

The larva is of the usual geometrid type having prolegs only on the sixth and the last abdominal segments, thus causing it to "loop" when bringing its abdomen forward while walking (Fig. 9a). The body lacks prominent protuberances; the setae are inconspicuous.

Larvae have five instars; head widths of each larval stage are shown in Table 1. The larvae vary in length from 1.7 to 19.1 mm during their development.

Body color and pattern are fairly uniform during the first four instars after changing in the first instar from yellowish to frosty green. The fifth instar is variable in

Table 1. Head widths of *Stamnodes* larvae, 1979.

Instar	n	Head width (mm)	
		Mean	Minimum-Maximum
I	30	0.35	0.31-0.39
II	30	0.59	0.54-0.65
III	30	0.87	0.82-0.97
IV	30	1.21	1.13-1.30
V	30	1.81	1.71-1.94

color (cover; Fig. 9) and includes a typical greenish form and darker forms as described later.

A remarkable feature of larvae is their chalazae (cone-like protrusions on the integument), each of which bears a single seta, pointing either forward or backward—and which in some instars has prongs, visible under magnification. The chalazae undergo certain instar-specific changes as described later for each instar. Their setae do not change much in length, so the setae become even less prominent in each successive instar.

The direction that setae point (either forward or backward) is constant in all instars but varies by body segment and location thereon. All of the thoracic setae point forward. On the first abdominal segment (A1) all point forward except the rearmost dorsal seta (D2). On A2-4, D1 and D2 are backward but all other setae are forward; on A5-6, D1, D2 and all lateral setae are backward except the subdorsal setae which point forward. Thereafter, setae on all segments point backward.

First Instar

Length, 1.7-3.5 mm; initially translucent light yellow but turning greenish with feeding. The body is lightly clothed with transparent setae arranged in longitudinal rows. The chalazae are fleshy and of the same color as the integument. The setae are transparent, glass-rodlike with amber bases. The head is almost heartshaped, being smoothly rounded and tapering toward the jaws, and is the color of the body. The epicranial lobes are faintly marbled above the ocelli, which are distinct and black. The crochets form a uniordinal mesoseries, containing 6 to 10 functional (hooked) crochets, interrupted in the middle by approximately 5 short, nonfunctional crochets.

Second Instar

Length, 2.2-5.5 mm; slightly darker green than instar I. Under magnification, vague cream stripes appear to run the length of the body. The integument

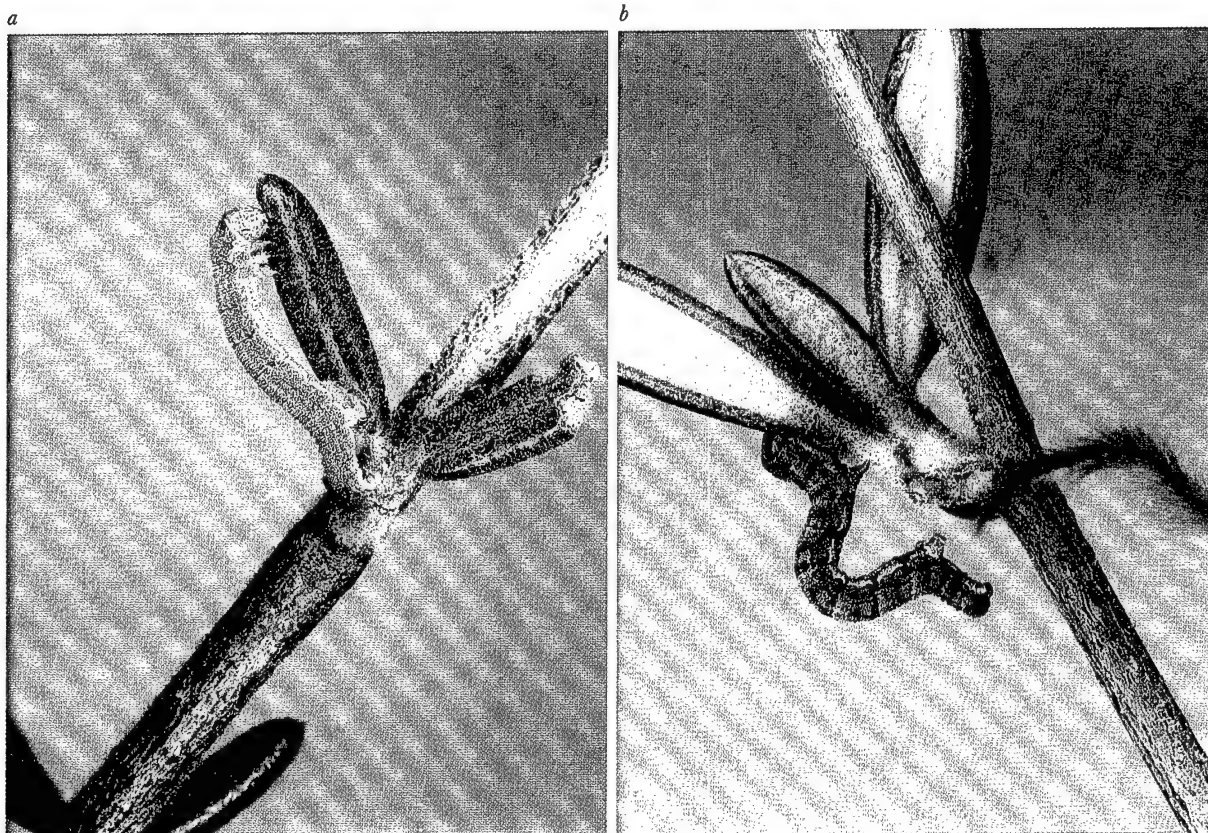


Fig. 9. Mature larvae varied in color. Most common was a greenish type (a) but others had a reddish color (b), or were melanistic (cover).

is more coarsely textured, consisting of tiny transparent pimples everywhere, with creamy white granules beneath the cuticle.

Each chalaza is developed dramatically into an upright peg which has a hornlike basal prong that points away from the seta. The prong is usually bifid and sometimes trifid, but this feature is not easily seen in this instar. The chalazae are glassy and as yet are unpigmented although they may turn cloudy in larvae about to molt.

The head is now subquadrate, becoming relatively broader in subsequent instars. Its marbling is slightly more distinct.

Crochets are relatively unchanged but may number from 8 to 12 and the spatula on the anal proleg is amber and more prominent.

Third Instar

Length, 4.2–7.8 mm; green coloration is unchanged, but the white lines along the length of the body are more evident to the unaided eye. Under magnification, the tiny cuticular pimples are no longer transparent and

each supports a whitish bristle. The chalazal bases are whitened internally, as are their prongs, some of which are bifid and even trifid.

The epicranial lobes of the head are prominently marbled and the head has become still more squarish. About 20 hooked crochets occur on the prolegs, forming a biordinal mesoseries that is interrupted in the middle by only 2 nonfunctional crochets.

Fourth Instar

Length, 7.4–11.6 mm; coloration is unchanged except for addition of scattered, minute, black dots dorsally along the body, as seen with the unaided eye. Under magnification, these are actually the chalazae, which now are stained black around the bases of the setae, a prominent characteristic of this instar. Also prominent are the whitish, bristle-bearing pimples that are spread densely over the body.

The head is less squarish and the sides are more broadly rounded. Its distinct markings are similar to those of instar III. The crochets now number 32 to 37 and consist of a triordinal mesoseries that forms a par-

tial circle. They appear unbroken, but one or two short, nonfunctional crochets occur at the middle, dwarfed by the hooked ones around them.

Fifth Instar

Length, 10.9–19.1 mm; consisting of several color phases with the highly variable markings and bandings (*cover*; Fig. 9)—so much so, that persons unfamiliar with the insect could mistake them for different species.

The typical larva is light green above except for a lateral white band, and is white on its underside. A melanistic color phase exhibits a medley of black, gray, tan, and white longitudinal bands, paired spots and chevrons, and dorsal saddles. Most of these darker larvae have a dorsal pattern reminiscent of a wolf's face imprinted on each abdominal segment I–V, against a black background. Between these color phases are intermediate forms often having a reddish cast.

The chalazae are reduced to mere black buttons supporting a transparent bristle. The prongs are absent and the chalazae are tiny in comparison with the body size.

The head is proportionally slightly wider than instar IV but is otherwise similar. Its background color ranges from shiny pearl to aged ivory and the marbling varies from amber to nearly black depending on the larval color-morph.

The crochets are unchanged from instar IV except they number 36 to 40 and all are functional. They are densely packed together; the ones of each different size are flared out in rowlike fashion, but microscopic examination shows their footing to be in one continuous line (mesoseries).

Pupa

The female pupa (*cover*) is slightly larger and proportionately broader than the male. Females average 9.6 mm long (SD = 0.69 mm, $n = 20$); males average 9.4 mm long (SD = 0.71 mm, $n = 20$). Their respective length to width ratios are 2.92:1 and 3.11:1. The only other major difference involves the genital opening, which in the female is porelike and spans the eighth and ninth abdominal segments, whereas in the male it has an elevated border and is located entirely on the ninth segment.

Pupae vary in color. Freshly transformed individuals have either a green head, thorax, and wings, and a yellowish abdomen; or they are uniformly yellowish brown. Some overwintered individuals may remain green, but mature pupae tend to be more uniformly brown.

In side view, the tenth abdominal segment is sharply constricted and reduced in size. The cremaster consists simply of two, 0.3-mm-long setae, often crossed near their tips, which arise from sclerotized wartlike bases. Another pair of smaller setae occur subapically of the larger pair.

Life History and Behavior

Adults

Moths were present on 23 May 1979. A few were still present on 9 July, at which time they appeared rubbed and spent. Peak abundance and activity occurred during the last 2 weeks of June. Adult presence was similar in 1980, but cooler weather resulted in a few moths being seen as late as 17 July.

Moths began emerging soon after dark and rested with wings hanging downward (*cover*) from any handy perch to which they crawled. Copulation (Fig. 10) was observed between 2300 h and midnight on 27 June 1979 and doubtless occurred before and after those hours. Mating pairs were all within 1 m of the ground. Mating occurred before flight.

In daytime, moths flew readily when approached to within 5 m. On such occasions, flight was rapid, erratic, and of brief duration. In calm air, moths tended to re-align on the same tree. In wind, they flew downwind, abruptly terminating flight by catching onto a branch with their legs, rather than hovering to a landing. At rest, they invariably held their wings closed above their back and hung downward.

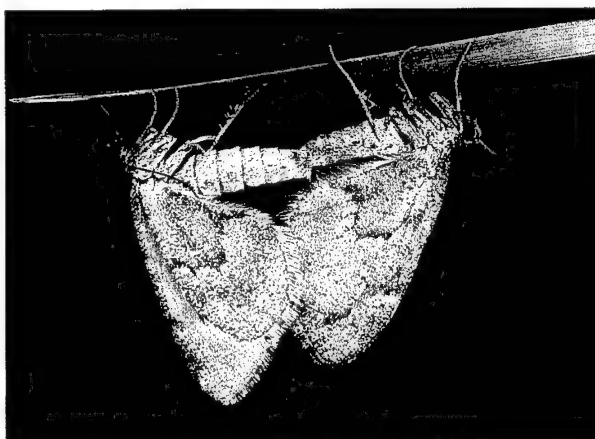


Fig. 10. Moths (*Stamnodes animata*) mated soon after emerging from soil at night. Color of moths varied from melanistic (*cover*) to brownish. The sexes are similar, but the male (right) has compressed, setose antennae.

Oviposition was not observed in the field and is believed to occur after dark. Moths were strongly attracted to ultraviolet light but not to visible incandescent light.

Eggs

Eggs were observed first on 9 June 1979. Oviposition rate appeared to be maximum during the latter half of June, as judged by moth abundance. Females laid eggs invariably on the pubescent undersides of leaves (cover; Fig. 8a) in groups varying from 1 to 40 (average, 9.5) based on observation of 243 egg-bearing leaves in 1979. Eggs were attached to leaves with the micropyle (Fig. 8b) facing away from the leaf, in bunches—rarely in rows—often touching each other. Although moths were flushed from other vegetation, including bitterbrush, *Purshia tridentata* (Pursh) DC, careful examination failed to locate eggs or larvae on vegetation other than mountain-mahogany. The eggs of 13 females, laid in June on potted plants in a greenhouse at Moscow, Idaho, hatched in an average of 18.8 days (range, 16–27 days).

Larvae

Larvae were present in the field from 26 June to 16 October 1979, but their abundance diminished rapidly after 1 October. The proportions of the five larval instars at weekly intervals are shown in Table 2.

The larvae are solitary. First instars fed on the upper leaf surface, causing a pitted appearance. Later instars notched the sides of the leaves, as is typical of geometrids. Entire leaves were rarely consumed. Larvae were difficult to detect because of their protective colors, their tendency to remain quiet, and their resistance to being dislodged. Often, when a clutch of hatched eggs was located on a leaf, we were unable to account for

the former occupants on distal branches. Larval webbing glistening on tree tops on 28 June 1979 caused us to speculate that some first instars may be wind-dispersed. However, that was never determined, and such behavior doesn't seem obligatory, judging from larvae that were reared on potted plants.

Pupae

Pupation evidently occurred mostly during the latter half of September based on observations of related activity as follows. On 16 September 1978, the silk of larvae abandoning trees was so abundant as to annoy persons camped among mahogany at Catnip Mountain, about 26 km north of Badger Mountain (Donald A. Klebenow, University of Nevada, personal communication). Larval collections on 19 September 1979 and 25 September 1981 contained virtually all mature larvae. On 2 October 1979, larvae were estimated to be only one-tenth as abundant as 2 weeks earlier, and an average of only one larva per beating was collected 16 October—one-fifth of the number in the week before.

Pupae occurred only in the upper 7 cm of soil, most commonly associated with roots of Idaho fescue (*Festuca idahoensis* Elmer). They required exposure to winter temperatures before maturing to adults, primarily in June.

Population Sampling

Adults

The presence and relative abundance of *S. animata* moths are easily determined in a locality by operating an ultraviolet light for an hour or so beginning at dusk. The date of such a survey should be timed to occur when most adults are active, which in the study area was

Table 2. Percentage of Stamnodes in each larval instar by collection date, Badger Mountain, Sheldon National Wildlife Refuge, Nevada, 1979.

Instar	June		July				August				September				October		
	28	2	9	16	23	30	6	13	20	27	3	10	17	24	2	10	16
I	100	100	71	8	4	2											
II			29	91	95	84	1	1	1								
III				1	1	14	97	95	81	3	2						
IV							2	4	18	95	83	16	3		2		
V										2	15	84	97	100	98	100	100
n	48	102	109	98	105	101	104	110	113	114	105	167	124	120	132	79	25

during the latter half of June. For example, between 2130 h and 2230 h on 27 June 1979, well over a thousand *S. animata* were attracted to an ultraviolet light at Badger Mountain. By comparison, on 21 June 1981, only 70 *S. animata* were attracted during a similar time period, reflecting the decline in their abundance. Similarly, only 12 *S. animata* were attracted in a mountain-mahogany stand west of Hines, Oregon, between 2115 h and 2230 h on 26 June 1981. We cannot help but wonder what our tally would have been if we had been lucky enough to have operated the light on Badger Mountain during June 1978! No doubt the impending defoliation would have been easy to forecast.

Eggs

Though they are not conspicuous, whatever their abundance, the eggs are a useful stage for measuring *S. animata* abundance. Furthermore, the appearance of eggs, including the nature of emergence holes in them, makes it possible to measure survival (hatch) and mortality (parasitism and nonviable).

A representative sample of eggs should be obtained after completion of oviposition, about the end of July. Using diagnostic features given in the section, "Natural Control, Egg Parasites," the eggs can be categorized and the rate of survival determined. Although we had no opportunity to relate density and survival of eggs to defoliation, the information given here will permit investigation of this point in the future, should, for example, light trapping indicate an impending outbreak.

Larvae

The larval stage is easy to census, but occurs later than the egg stage and, therefore, provides less advance warning of subsequent damage. Nonetheless, should other population measures not be available, or if censusing is continuing from an earlier stage, sampling larvae is practical and useful.

In 1980, we compared two methods: (1) Clipping (Fig. 5a) about 76 cm of branches (3 such samples from each of 10 different trees, weekly), and (2) beating (3 strikes per branch and 3 samples per tree; Fig. 5b). During 13 weeks of sampling, clipping produced an average of 79.1 loopers (SD = 39.5) per week, whereas beating produced 255.1 (SD = 212.5). However, we noted that, during the first 6 weeks (14 July–18 August), while loopers were small (second and third instars), clipping produced more loopers than did beating (average, 76.0 vs. 59.2). This difference was due to young larvae being more tenacious, a characteristic related to their

smaller mass and perhaps the substrate to which they were attached. In any event, if samples are taken before the fourth instar, one should clip and examine at least some branches to compare with those obtained by beating.

Another caterpillar (*Ethmia discostrigella* Chambers) is common on mountain-mahogany and will be encountered while sampling. It made up 21.3% of the Lepidoptera larvae collected by beating in 1979. So far, we know of no documented instance where it alone caused mahogany mortality, but it was fairly abundant in both this looper outbreak and that of *Anacamptodes clivinaria profanata* (Barnes and McDonnough) in Idaho (Furniss and Barr 1967).

Pupae

The pupal stage was not suited to sampling because pupae intermingled with roots of understory vegetation, especially Idaho fescue. This behavior contrasted with that of *Anacamptodes* in Idaho, which was easily censused by sifting the root-free soil of that area through screens (Furniss and Barr 1967). We did, however, painstakingly count 143 pupae in the upper 7.6 cm of soil from an area of about 0.5 m² on 23 May 1979. Should pupae be sought (e.g., for rearing tachinid parasites), the best method is to dig up grass roots with a shovel, then separate them while watching for pupae to fall out.

Natural Control

Ants

In May 1979, the mountain-mahogany stands posed a bleak sight. Refoliation had not yet commenced and the patches of gray trees formed a somber mosaic amidst a background of sagebrush and earth. Yet, here and there, normal-appearing mountain-mahogany trees stood out. These unscathed trees were examined and found to be infested with a soft scale (*Parthenolecanium corni* complex (Bouche); Fig. 11), which were tended by ants seeking honeydew (Way 1963).

The ants (*Formica integroides planipilis* Creighton) were traced backward along their trails to their nests, varying from a few meters to 24 m away. Species of *Formica* are important predators of defoliating forest insects (Youngs 1983) and the entrance to their nest consists of a mound of sticks and leaves (Fig. 6a).

Because we consistently found *Parthenolecanium* scales on undefoliated trees, also characterized by the sooty appearance of their branches, we set up an experiment as follows. Ten *Stamnodes* loopers were placed weekly on



Fig. 11. Some mountain-mahogany trees were infested with shell-like female *Parthenolecanium* scales that attracted predatory *Formica* ants to their secreted honeydew. The ants preyed on loopers and kept the trees green.

each of four scale-infested branches, two branches of which were ringed with adhesive to exclude ants. Of 440 loopers put onto each category of branch (Table 3), only two were counted subsequently on branches where ants were free to roam—a reduction of 98.4% compared with the ant-free branches. Predation was doubtless involved, but we also noted some loopers hanging on silk threads, apparently having been dislodged by ant activity.

After the decline of the *Stamnodes* population in 1980, surviving trees gradually refoliated and stood out from trees that died or that contained dead stems. Furthermore, the green trees were abundant at higher elevation, whereas dead trees were more abundant at lower elevation (Fig. 12). Observations led to discovering that *Formica* ant nests were dominant in the greener, higher area, whereas harvester ant nests (*Pogonomyrmex owyheei* Cole) prevailed among the dead or damaged trees lower down. *P. owyheei* is a ground dweller that forages mainly for seeds (Willard and Crowell 1965). It heaps fine

gravel around the nest entrance, and removes surrounding vegetation (Fig. 6c).

We therefore set out to survey the condition of mahogany trees by elevation and proximity to nests of either species of ant (Table 4). At lower elevations (1,933–1,951 m), *Pogonomyrmex* made up 95.7% of ant mounds visible from sample trees; 76.3% of the trees were dead or had at least half of their crowns killed. At the higher elevations (2,104–2,165 m), *Formica* was the only mound-builder and its presence was reflected by a reverse relation; that is, 82.3% of the trees were undamaged or more than half of their crowns were alive.

Ichneumonidae

Black eggs of a parasitic wasp of the subfamily Tryphoninae (probably *Netelia* sp.) were found on *Stamnodes* larvae beginning 27 August 1979 and beginning 25 August 1980. Of 233 parasitized loopers examined, all were in their fourth and fifth instars except one that was in the third instar.

The egg is black, 0.7 mm long \times 0.35 mm wide, somewhat oval in form, but flattened on the underside. The shell is tough and smooth except ventrally and at the two ends, which have minute, beadlike warts.

Eggs are anchored to loopers by a filament (petiole) which has an enlarged thorn-tipped end. Female tryphonine wasps are unique in carrying their eggs on their ovipositor (Clausen 1940) and inserting the petiole through the host larva's integument, thereby holding the egg shell fast until the parasite larva becomes free-living.

The biology of the wasp on *S. animata* is similar to that of *Netelia* (*Netelia*) *spinipes* (Cushman) as published by Vance (1927). The first stage wasp larva is 0.08 mm long, and whitish except for its large, shiny brown head capsule. It attaches itself to the looper's integument with two sharp, hornlike mandibles that are about 0.08 mm long and curved inwardly. As the larva grows, the egg shell is pushed open increasingly more. The shell continued to be used for shelter until as late as early October when the occupant became too big and thereafter clung to the host by its mouth parts. The ultimate instar was whitish and glistening smooth, without a sclerotized head or any fleshy appendages. The mouthparts are those typical of Tryphoninae (Short 1978; Finlayson and Hagen 1978).

We believe that the parasite larva either accompanies the looper host to the ground, or drops to the ground, and that the parasite overwinters as a larva in a cocoon. The only cocoon observed was 1.2 \times 0.4 cm, rounded at its ends and circular in cross section; its exterior was

Table 3. Number of *Stamnodes* larvae present on two ant-free and two ant-exposed branches following releases of 10 larvae per branch per week, Badger Mountain, Sheldon National Wildlife Refuge, Nevada, 1980.

Observation date ^a	Instar	Number of larvae			
		<i>Formica</i> excluded		<i>Formica</i> present	
		1	2	3	4
August 4	2	2	0	1	0
11	2, 3	3	3	0	0
18	3	6	11	1	0
25	3, 4	5	5	0	0
September 2	3, 4	8	11	0	0
8	3, 4	10	10	0	0
15	4, 5	8	7	0	0
22	4, 5	8	8	0	0
29	5	7	6	0	0
October 6	5	1	1	0	0
14	5	2	2	0	0
Total		60	64	2	0

^aTen larvae were placed on each branch beginning 28 July and ending 6 October. Larvae present were counted each subsequent week, before new larvae were placed onto branches.

black and hairy. The presumed adult is known to us only from a female specimen beaten from foliage 22 September 1980.

Characteristics and Rates of Parasitism

Of 33 parasitized loopers collected 7 October 1980, 82% had one egg, 15% had two eggs, and 3% had three eggs each. Eggs were attached only to thoracic segments of loopers, never to their head or abdomen. A majority of eggs were laid in intersegmental folds and 90% oc-

curred forward of the metathoracic segment. Loopers of green or melanistic color were parasitized about equally (25 and 27%, respectively).

Rates of parasitism for 3,635 loopers of the final three instars are given in Table 5 for 1979 and 1980. Of 651 third instar larvae, only one contained a black egg. Rates of parasitism were higher each year in the fifth than in the fourth instar, and increased in both instars by severalfold in 1980, compared with 1979. Although we purposely collected and examined more loopers in

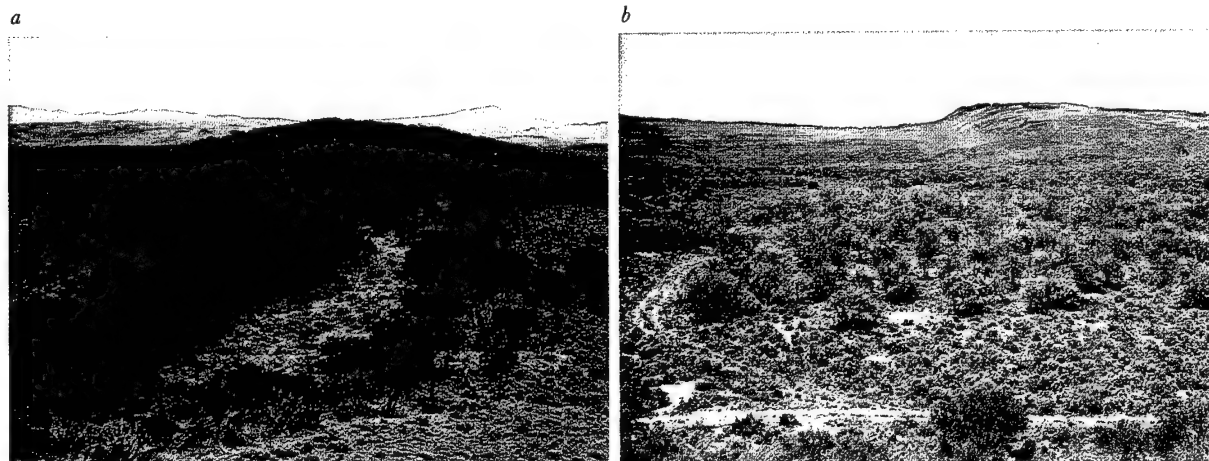


Fig. 12. Mountain-mahogany stands at higher elevation (a) recovered from defoliation rapidly. At lower elevation (b), most trees died.

Table 4. *Severity of defoliation-caused damage to C. ledifolius trees in relation to elevation and density of mounds of Formica and Pogonomyrmex ants, Badger Mountain and Fish Creek Mountain, Sheldon National Wildlife Refuge, Nevada, 1982.*

Elevation (m)	Number of trees sampled	Number of mounds		Frequency of damage class (%)			
		<i>Formica</i>	<i>Pogonomyrmex</i>	Green	<50%	>50%	Dead ^a
2,104–2,165	340	60	0	58.2	24.1	6.2	11.5
2,073–2,104 ^b	312	42	0	47.4	31.7	7.4	13.5
1,963–2,012	548	12	76	15.3	35.4	20.3	29.0
1,933–1,951	668	5	112	3.6	20.1	20.2	56.1
Total	1,868						

^a22.9% of this class appeared to have been dead before 1978, presumably because of an earlier outbreak.

^bLocated on Fish Creek Mountain; others were located at Badger Mountain.

Table 5. *Rate of parasitism of Stamnodes larvae by Netelia sp. (Ichneumonidae), Badger Mountain, Sheldon National Wildlife Refuge, Nevada, 1979–80.*

Date		Instar III		Instar IV		Instar V	
		Number examined	Parasitized (%)	Number examined	Parasitized (%)	Number examined	Parasitized (%)
1979							
August	20	92	0	20	0	0	0
	27	4	0	108	0.9	2	0
September	3	2	0	87	1.1	16	6.2
	10			26	0	141	4.3
	17			4	0	120	2.5
	24					120	1.7
October	2			2	0	130	6.9
	10					79	5.1
	16					25	28.0
Total		98		247		633	
Average			0		0.8		5.1
1980							
August	19	145	0	2	0		
	25	257	0.4	75	1.3		
September	3	94	0	374	7.0	6	16.7
	9	57	0	477	5.2	52	25.0
	16			236	5.9	263	17.9
	22			17	0	238	5.9
	29			2	0	233	10.3
October	7			1	0	128	25.8
Total		553		1,184		920	
Average			0.2		5.6		14.3

1980, the field population was smaller, as judged by much less damage compared with 1979. Lesser abundance of loopers may have resulted in relatively more of them having been parasitized, compared with 1979.

The only occurrence of an egg on another host species was on a gelechiid caterpillar collected 15 July 1980. It had one egg on its thorax. This record predates by 41 days our earliest collection of a parasitized *Stamnodes* larva in 1980. Possibly the egg on the gelechiid was that of another, similar ichneumon, or perhaps the wasp bridges across summer on lepidopterous hosts as one species pupates and another develops to susceptible size. However, we never observed a black egg on *Ethmia discostrigella* larvae, which were second in abundance to *Stamnodes*.

Tachinidae

Overwintering *Stamnodes* pupae contained two species of tachinid flies (*Patelloa pluriseriata* (A & W) and *Blondelia connecta* (Curran)). Those pupae were doubtless parasitized while in the larval stage. The latter species was

rare and was represented by only three adults, reared from host pupae collected 20 November 1978.

Because systematic sampling of *Stamnodes* pupae was impractical (see "Population Sampling"), we have only limited information on the rate of parasitism by tachinids. We did, however, rear 223 pupae that were collected from underneath 20 trees between 4-8 June 1979, a time when pupae were still abundant (Table 6). All of the emerged tachinids appeared to be *P. pluriseriata*. They killed 16% of the pupae we collected, equal to about half the number of pupae that produced adult *Stamnodes*. A slight majority (53%) of collected pupae died from an unknown cause.

Patelloa pluriseriata adults emerged at room temperature during 27 June to 14 July 1979 from pupae collected 4-8 June. Adults were abundant around mahogany trees at Badger Mountain on 22 August 1980. They were also abundant in flight in late morning 25 August 1980 around a rocky prominence on top of a small mountain at 2,090 m (6,857 feet) elevation.

The evident disparity between time that tachinids emerged in June and availability of mature *Stamnodes*

Table 6. *Survival, tachinid parasitism, and unknown mortality of Stamnodes pupae, Badger Mountain, Sheldon National Wildlife Refuge, Nevada, June 1979.*

Tree number	Number of pupae	<i>Stamnodes</i> emerged			Parasitized by <i>Patelloa</i>	Dead pupae
		♀	♂	Total		
1	11	2	1	3	3	5
2	10	3	1	4	1	5
3	10	3	1	4	2	4
4	14	0	0	0	2	12
5	11	2	0	2	0	9
6	10	3	2	5	0	5
7	11	2	2	4	1	6
8	11	1	1	2	2	7
9	10	0	0	0	2	8
10	22	2	4	6	4	12
11	10	5	3	8	1	1
12	10	1	1	2	3	5
13	11	4	3	7	0	4
14	10	3	3	6	2	2
15	10	2	1	3	3	4
16	10	3	0	3	2	5
17	10	1	0	1	1	8
18	10	2	0	2	0	8
19	12	1	3	4	6	2
20	10	2	1	3	0	7
Total	223	42	27	69	35	119
Percent				31	16	53

larvae in late August indicates that the adults are fairly long-lived. How they were sustained during that period was not evident, but we wonder if their sustenance could be related to secretions of *Parthenolecanium* scales, there being no more obvious source of liquid or nutrition.

Egg Parasites

Between 30 June and 12 August 1980, 2,181 *Stamnodes* eggs were collected to identify their parasites. We reared three species of wasps from them: a scelionid (*Telonomus* sp.) and two trichogrammatids (*Trichogramma exiguum* Pinto and Platner and *T. pretiosum* Riley). The *Telonomus* sp. was solitary; from one to three *Trichogramma* emerged per egg.

The fate of each *Stamnodes* egg was diagnosed symptomatically as follows.

- Shell whitish; end with a large, clean exit hole *Stamnodes*
- Shell whitish; end with a large, somewhat ragged hole; solitary black parasite, 0.7–0.9 mm long *Telonomus*
- Shell grayish; minute hole in upper side or top; multiple amber parasite, 0.3–0.5 mm long *Trichogramma*
- Shell usually grayish, sometimes orangish; without any exit hole (nonviable) Unknown

The peak rate of parasitism of eggs by *Telonomus* preceded that of *Trichogramma* (Table 7). In combination, the wasps killed 43.6% of the eggs, as judged by wasp exit holes in them, and they may have been a factor in a sizable proportion of eggs (40.5%) from which neither *Stamnodes* nor wasps emerged. Whatever the

case, egg parasites became an important controlling force as the *Stamnodes* population waned.

Effects of Defoliation

Mountain-mahogany

Rates of tree mortality and partial killing of trees varied with elevation, and were influenced mainly by severity of defoliation—a factor correlated negatively with *Formica* ant abundance (Table 4). Stands at lower elevations suffered 29.0 to 56.1% mortality compared with 11.5 to 13.5% at higher elevations. The frequency of green, undamaged trees was only 3.6% in low elevation stands versus 58.2% at high elevation.

Of our sample of 1,868 trees from all elevations, 43% were partially killed; that is, had one or more trunks or outer branches killed. Some of the partially killed trees may die prematurely from infestation by wood borers and infection by fungi.

Some defoliated trees developed a gouty-appearing new growth, particularly evident in spring 1980 (Fig. 13). These trees lost their gouty look in subsequent years but developed bushier-than-normal crowns. We believe that the gouty growth-form may have resulted from looper feeding that killed the apical bud of each such branch, although that was not actually observed.

A further effect of looper feeding was the loss of fruit production on completely defoliated trees in 1979 and 1980. Lack of fruit was likely due to loopers eating reproductive buds in late summer in 1978 and 1979 when the loopers had attained damaging size. Casual observation disclosed that fruit production continued normally on undamaged trees.

Table 7. Rates of parasitism of *Stamnodes* eggs by *Telonomus* and *Trichogramma* wasps, Badger Mountain, Sheldon National Wildlife Refuge, Nevada, 1980.

Collection date	Number of <i>Stamnodes</i> eggs	Parasite (%)	
		<i>Telonomus</i>	<i>Trichogramma</i>
June 30	346	50.6	
July 7	470	41.1	
15	327	45.0	6.4
22	336	4.2	16.4
28	379	17.4	16.6
August 5	209	19.1	50.7
12	114	10.5	50.9
Total	2,181	29.7	13.9



Fig. 13. Some mountain-mahogany trees that survived defoliation developed a temporary gouty appearance.

Passerine Birds

Sixty-one species of birds were recorded on the four mountain-mahogany transects during 1978–84 (Table 8). Fifty-two species occurred on Fish Creek Mountain and 36 occurred on Badger Mountain. Twenty-four species occurred only on Fish Creek Mountain and 9 species occurred only on Badger Mountain, with 28 species common to both sites. Of the 28 species occurring on both sites, 10 emerge as “site indicators” (Table 9), as judged by their fidelity to the mountain-mahogany sites, including breeding there. These are the gray flycatcher (*Empidonax wrightii*), scrub jay (*Aphelocoma coerulescens*), Brewer’s blackbird (*Euphagus cyanocephalus*), vesper sparrow (*Poocetes gramineus*), Brewer’s sparrow (*Spizella breweri*), green-tailed towhee (*Pipilo chlorurus*), sage thrasher (*Oreoscoptes montanus*), bushtit (*Psaltiriparus minimus*), blue-gray gnatcatcher (*Polioptila caerulea*), and American robin (*Turdus migratorius*).

Fish Creek Mountain

Scrub jay and sage thrasher appeared to be maintaining a fairly stable population—neither increasing nor decreasing (Table 9). Counts of eight species indicated

a population increase during most years after the 1978 defoliation: gray flycatcher, bushtit, vesper sparrow, Brewer’s sparrow, green-tailed towhee, blue-gray gnatcatcher, Brewer’s blackbird, and American robin. No key site-indicator species portrayed an overall downward trend although all but the vesper sparrow and Brewer’s sparrow were less abundant in 1980 and 1982 after a severely cold, wet weather occurred during nesting.

Badger Mountain

Two species (sage thrasher and blue-gray gnatcatcher) did not appear with enough frequency to determine a trend. Two species that appeared to be stable were the bushtit and vesper sparrow; however, the latter occurred in low numbers. Two species (Brewer’s blackbird and Brewer’s sparrow) increased markedly between 1978 and 1984. Green-tailed towhees increased slightly and scrub jays decreased slightly. Two species disappeared from transects: gray flycatcher, never abundant, decreased 3 consecutive years (1978–80) and disappeared thereafter; and American robin, after a threefold increase from 1978 to 1979, gradually diminished in numbers and disappeared in 1984 (Table 9).

Late spring snow storms frequently occur in Sheldon NWR at higher elevations. Timing and duration of these storms are critically important to passerine birds by limiting insects available for food and lowering their nesting success. Sharp declines in bird densities, existing only for 1 year, generally signify such a weather effect. In 1980, 6 of the 10 indicator species portrayed such an impact (Table 9). In 1982, declines in the abundances of 8 of the 10 indicator species suggested that inclement weather in spring of that year again reduced breeding populations.

In summary, Fish Creek Mountain has recovered better from the defoliation (89.5% mahogany survival) and despite occurrence of adverse weather during the breeding seasons of 1980 and 1982, small-bird densities have steadily increased. In contrast, the mahogany trees on the Badger Mountain transect have not recovered as well (43.9% mahogany survival). The understory vegetation at Badger Mountain, however, has improved and supports an increased abundance of Brewer’s blackbird and Brewer’s sparrow. The loss of the mahogany canopy is the main contributor to the decline in diversity and the loss from the Badger Mountain site of the gray flycatcher and American robin, and the decline in scrub jay numbers. American robins and jays (Fig. 14) require the well-foliated branches of the mahogany for nesting. The gray flycatcher, although primarily nesting in low brush, is dependent on living mahogany as

Table 8. *Common names of passerine birds recorded on four 10-ha transects, Sheldon National Wildlife Refuge, Nevada, 1978-84.*

Bird species	Location ^a	Bird species	Location
American kestrel ^b	FC	Townsend's warbler	B
Black-headed grosbeak	FC	Warbling vireo	B
Black-throated sparrow	FC	White-crowned sparrow	B
California quail	FC		
Dark-eyed junco	FC	American robin ^c	FC, B
Dusky flycatcher	FC	Blue-gray gnatcatcher ^c	FC, B
Golden eagle	FC	Brewer's blackbird ^c	FC, B
Lazuli bunting	FC	Brewer's sparrow ^c	FC, B
Macgillivray's warbler	FC	Brown-headed cowbird	FC, B
Mountain chickadee	FC	Bushtit ^c	FC, B
Northern harrier	FC	Cassin's finch ^b	FC, B
Prairie falcon ^b	FC	Chipping sparrow	FC, B
Sage grouse	FC	Common raven	FC, B
Savannah sparrow	FC	Gray flycatcher ^c	FC, B
Say's phoebe	FC	Great-horned owl ^b	FC, B
Song sparrow	FC	Green-tailed towhee ^c	FC, B
Townsend's solitaire	FC	Horned lark ^b	FC, B
Western flycatcher	FC	Long-eared owl ^c	FC, B
Western kingbird	FC	Mountain bluebird ^c	FC, B
Western tanager	FC	Mourning dove ^b	FC, B
Western wood pewee	FC	Northern flicker ^b	FC, B
White-throated swift	FC	Red-breasted nuthatch	FC, B
Wilson's warbler	FC	Red-tailed hawk ^b	FC, B
Yellow warbler	FC	Rock wren ^c	FC, B
		Ruby-crowned kinglet	FC, B
Black-billed magpie ^b	B	Rufous-sided towhee	FC, B
European starling	B	Sage sparrow	FC, B
Lark sparrow	B	Sage thrasher ^c	FC, B
Loggerhead shrike	B	Scrub jay ^c	FC, B
Plain titmouse	B	Vesper sparrow ^c	FC, B
Rough-winged swallow	B	Violet-green swallow	FC, B
		Western meadowlark ^b	FC, B

^aFC = Fish Creek Mountain; B = Badger Mountain.^bKnown to nest within mountain-mahogany sites.^cNest found on transect.

a source of insects for food and for perching while feeding on insects caught in the surrounding air.

Soil Enrichment and Litter Deposition

In 1980, 2 years after the outbreak occurred, total nitrogen (TN) was 6 times higher under either defoliated or undefoliated trees than in nearby openings. Studies of other desert shrubs have usually shown a threefold difference between undercanopy and open locations (Tiedmann and Furniss 1985). Furthermore, TN in our mountain-mahogany soil samples was about twice that reported for soil from another Nevada mountain-mahogany stand (Lepper and Fleschner 1977).

Due to the likelihood of N from looper excrement having leached from the soil surface since 1978, we believe that the elevated N in 1980 was more likely the result of redistribution from open areas via tree roots. Also, mountain-mahogany contains root nodules that harbor N-fixing bacteria (Youngberg and Hu 1972) which may have added to the content of N beneath the mahogany.

Litter increased 1,186 g/m² beneath defoliated trees compared with nondefoliated trees. The increased leaf deposition was due to the loopers' inefficient feeding, which resulted in their notching leaves, rather than consuming them. That caused the damaged leaves to desiccate and drop prematurely; undamaged leaves are retained for 2 years or longer. We did not investigate

Table 9. Average number of key site-indicator birds encountered per day, Fish Creek Mountain and Badger Mountain transects, 1978-84.

Bird species	1978		1979		1980		1981		1982		1984	
	Fish Cr.	Badger	Fish Cr.	Badger	Fish Cr.	Badger	Fish Cr.	Badger	Fish Cr.	Badger	Fish Cr.	Badger
Gray flycatcher	0.2	0.3	0.6	0.3	0.1	0.1	1.7	0	0.6	0	3.4	0
Scrub jay	1.3	1.8	1.0	3.4	1.0	3.5	0.7	5.0	1.3	0	1.0	2.0
Bushtit	0	0.9	0.1	0.2	0.2	0.2	1.4	0.5	0	0	1.2	1.0
Brewer's blackbird	8.8	0.6	26.9	2.6	15.6	2.5	17.0	3.7	10.3	3.8	22.6	4.3
Vesper sparrow	1.0	0	1.2	0.1	0.9	0.1	1.4	0.1	3.0	0	0.6	0.1
Brewer's sparrow	1.8	1.0	8.1	2.3	3.4	3.8	8.3	1.4	9.3	3.4	11.1	3.7
Green-tailed towhee	1.3	0.2	0.7	0.9	1.8	0.7	3.4	1.0	0.6	0.4	3.9	0.3
Sage thrasher	0.3	0	2.7	0.3	0.9	0.1	0.9	0	1.6	0	1.0	0
Blue-gray gnatcatcher	0.8	0	1.1	0.7	0.9	0	0.6	0	0	0	6.3	0
American robin	1.3	0.3	5.2	3.1	3.5	2.4	3.3	1.3	2.3	1.2	4.9	0
Total	16.7	5.1	47.6	13.9	28.3	13.4	38.7	13.0	29.0	8.8	56.0	11.4



Fig. 14. Scrub jays (*Aphelocoma coerulescens*) require mountain-mahogany for nesting at Sheldon National Wildlife Refuge. They disappeared from transects where a majority of trees died.

the effects of this temporarily increased litter deposition but we visualize that surface-soil microclimate was enhanced with respect to soil organisms and seedling establishment. Supporting this possibility was a significantly lower S (sulfur) availability under defoliated trees relative to undefoliated trees. Lowered available S would be consistent with increased microbial activity.

Plant Community Response

Idaho fescue was common beneath the canopies of many mountain-mahogany trees at the time of the looper outbreak. Defoliation in 1978 was followed by release of fescue in subsequent years (Fig. 6a, background), possibly due largely to increased sunlight and available moisture. Less evident were short-term increases in percent canopy cover of components of the plant community on line intercept transects (Table 10). These measurements, however, included vegetation, in openings between mountain-mahogany trees, that may have been less influenced by removal of mahogany leaves. In the long term the question to be answered is whether and when mountain-mahogany trees will regain their former density.

Susceptibility Classification and Management

Curlleaf mountain-mahogany grows in diverse environments over a 10-State area. For example, in Oregon

Table 10. Proportional canopy cover of component species of the mountain-mahogany community at time of defoliation^a and 1 year later, Sheldon National Wildlife Refuge, Nevada, 1979 and 1980.

Plant species	Fish Creek Mountain canopy cover (%)		Badger Mountain canopy cover (%)	
	1979	1980	1979	1980
Shrubs				
<i>Cercocarpus ledifolius</i>	31.3	30.0	17.1	15.0
<i>Artemisia tridentata</i> var. <i>tridentata</i>	7.8	8.5	1.6	1.9
<i>Artemisia tripartita</i>	0.3	0.3	—	—
<i>Chrysothamnus viscidiflorus</i>	2.0	2.8	1.1	1.3
<i>Purshia tridentata</i>	0.8	2.5	2.2	1.9
<i>Symphoricarpos oreophilus</i>	1.3	1.4	—	—
<i>Ribes aureum</i>	—	—	0.7	0.7
Total	43.5	45.5	22.7	20.8
Grasses and sedges				
<i>Festuca idahoensis</i>	3.9	4.0	1.7	1.8
<i>Poa secunda</i>	0.4	0.5	0.6	0.8
<i>Sitanion hystrix</i>	0.4	0.5	0.5	0.6
<i>Agropyron spicatum</i>	0.5	0.5	T ^b	0.3
<i>Stipa thurberiana</i>	T	0.2	0.6	0.9
<i>Stipa webberi</i>	0.4	0.5	—	—
<i>Carex douglasii</i>	T	T	0.4	0.5
Total	5.6	6.2	3.8	4.9
Forbs				
<i>Mertensia longiflorus</i>	T	T	—	—
<i>Crepis acuminata</i>	0.2	0.3	T	T
<i>Balsamorhiza sagittata</i>	1.7	1.7	—	—
<i>Senecio integerrimus</i>	0.1	0.1	T	T
<i>Phlox longifolia</i>	T	T	T	T
<i>Microseris nutans</i>	T	T	T	T
Total	2.0	2.1	T	T

^a As measured in June 1979, before any evident change from defoliation in September 1978.

^b T = trace.

alone, mountain-mahogany grows in five physiographic divisions and occurs in 12 habitat types (Dealy 1975). The species of plants associated with mountain-mahogany doubtless influence the kinds and abundance of mahogany-infesting insects. For instance, phytophagous insects that are specific to plants associated with mountain-mahogany can serve as reservoirs (i.e., food) of parasites and of predacious *Formica* ants (Fig. 6b) during times when they cannot be sustained on mountain-mahogany insects alone.

Interwoven in the various mountain-mahogany ecosystems are the effects of climate and weather, and the steepness of ground and texture of soil on which individual trees and stands grow. Our observations of curleaf mountain-mahogany over distant parts of its range, and experience with outbreaks of two species of

geometrid defoliators, *Anacamptodes* (Furniss and Barr 1967) and *Stamnodes*, lead us to propose the following means whereby managers may classify mahogany stands according to their susceptibility.

Both looper outbreaks had in common very extensive, well-established, generally mature mountain-mahogany stands in which mahogany was dominant. Big sagebrush was the predominant surrounding vegetation. The sites were high desert steppe at elevations of about 1,800 m to 2,200 m. Topography was gentle to moderately steep; in the latter instance, aspects were predominantly cool-facing. Underlying parent rock was volcanic, and soil beneath trees was developed to a depth of several inches, permeable, and covered generously with litter consisting mainly of shed leaves. Such litter-rich, friable soil is essential for mature loopers to enter it and pupate.

The lack of litter-rich, friable soil in which to pupate limits the abundance of *S. animata* within much of the host plant's range. For example, mountain-mahogany is common in the Salmon River canyon in Idaho County, Idaho, but the steep and rocky terrain has poorly developed soil and lacks ample litter for successful pupation. But, even in other areas, where mountain-mahogany grows extensively on favorable soil, further stratification of susceptibility is possible. At Sheldon NWR, for example, we observed much less tree mortality above approximately 1,980 m (6,496 feet), where *Formica* ant nests were abundant, compared with lower areas where this predacious ant was lacking.

So, a resource manager can expect little geometrid-caused mahogany mortality where soil is bare or rocky and where trees are not extensive. And even in extensive stands on favorable soil, looper outbreaks may kill only a minority of defoliated trees that are amidst *Formica* ant colonies, as opposed to colonies of harvester ants that do not climb trees and prey on or dislodge loopers.

When susceptible stands lacking *Formica* ants are located, consideration should be given to introducing *Formica* species suited to the location. But, if no course of preventive action is feasible, we urge temperance should an outbreak occur. The stands involved have probably coevolved with the loopers. If management objectives permit it, patience will be rewarded in time by regeneration of a new stand, provided that seedlings and some survivors are present, as we found to be the case. The flush of growth on released understory grasses and other plants will provide some compensating benefit, but its use by ungulates will need monitoring to determine their effect on mountain-mahogany regeneration.

If, however, future technology should make available an effective, ecologically acceptable control treatment—such as a biological agent—prevention of defoliation in the year of outbreak seems necessary to forestall tree mortality. That is, once mature trees were completely stripped of their accumulation of leaves, mortality occurred. The extent to which mortality could be prevented by controlling the second looper generation is uncertain and would likely depend on age and vigor of trees. In any event, no one has yet detected a mountain-mahogany looper outbreak in time for such action.

To sum up, only a portion of the curleaf mountain-mahogany resource is at risk of looper damage. Susceptible stands can be identified and stratified by the criteria provided. Such stands have a potential for looper outbreaks with resultant severe tree damage and mortality, and perturbations in their associated flora and fauna. Until technology provides an effective, accept-

able applied control against a budding outbreak, it may only be possible to adjust animal use to utilize increased understory vegetation, and to let nature take its course. Gradually, a new stand will be established, as was likely the situation for millennia.

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Taxonomists of the Systematic Entomology Laboratory, USDA, who identified insects, were P. M. Marsh (*Telonomus*), A. S. Menke (Ichneumonidae), D. R. Miller (*Parthenolecanium*), C. W. Sabrowsky and D. D. Wilder (Tachinidae), D. R. Smith (*Formica*), and D. L. Vincent (*Trichogramma*). N. F. Johnson, Cornell University, also examined the *Telonomus*. Others who identified insects involved in the study were F. R. Merickel, University of Idaho, and S. O. Shattuck, University of Kansas (*Pogonomyrmex*); and K. S. Hagen, University of California, J. B. Johnson, University of Idaho, and T. R. Torgersen, Forest Service, USDA (*Netelia*).

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Key words: Defoliator, Geometridae, looper, *Stammodes animata*, curleaf mountain-mahogany, *Cercocarpus ledifolius*, susceptibility, natural control, ants, passerine birds.

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Furniss, Malcolm M., Douglas C. Ferguson, Kenneth W. Voget, J. Wayne Burkhardt, Arthur R. Tiedemann, and John L. Oldemeyer. 1988. **Taxonomy, life history, and ecology of a mountain-mahogany defoliator, *Stammodes animata* (Pearsall), in Nevada.** U.S. Fish Wildl. Serv., Fish Wildl. Res. 3. 26 pp.

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Key words: Defoliator, Geometridae, looper, *Stammodes animata*, curleaf mountain-mahogany, *Cercocarpus ledifolius*, susceptibility, natural control, ants, passerine birds.

The following is a list of recent *Fish and Wildlife Research* publications.

1. Life History and Status of the Endangered Cui-ui of Pyramid Lake, Nevada, by G. Gary Scoppettone, Mark Coleman, and Gary A. Wedemeyer. 1986. 23 pp.
2. Spread, Impact, and Control of Purple Loosestrife (*Lythrum salicaria*) in North American Wetlands, by Daniel Q. Thompson, Ronald L. Stuckey, and Edith B. Thompson. 1987. 55 pp.

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